Historical range of variability in live and dead wood biomass: a regional-scale simulation study

Etsuko Nonaka, Thomas A. Spies, Michael C. Wimberly, and Janet L. Ohmann

Abstract: The historical range of variability (HRV) in landscape structure and composition created by natural disturbance can serve as a general guide for evaluating ecological conditions of managed landscapes. HRV approaches to evaluating landscapes have been based on age-classes or developmental stages, which may obscure variation in live and dead stand structure. Developing the HRV of stand structural characteristics would improve the ecological resolution of this coarse-filter approach to ecosystem assessment. We investigated HRV in live and dead wood biomass in the regional landscape of the Oregon Coast Range by integrating stand-level biomass models and a spatially explicit fire simulation model. We simulated historical landscapes of the region for 1000 years under pre-Euro-American settlement fire regimes and calculated biomass as a function of disturbance history. The simulation showed that live and dead wood biomass historically varied widely in time and space. The majority of the forests historically contained 500–700 Mg·ha^{-1} (50–70 kg·m^{-2}) of live wood and 50–200 Mg·ha^{-1} (5–20 kg·m^{-2}) of dead wood. The current distributions are more concentrated in much smaller amounts for both biomass types. Although restoring the HRV of forest structure is not necessarily a management goal for most landowners and managing agencies, departure from the reference condition can provide relative measure to evaluate habitat conditions for managers seeking to use forest structure as a means to maintain or restore ecosystem and species diversity.

Résumé : L'étendue historique de la variabilité (ÉHV) dans la composition et la structure du paysage engendrée par les perturbations naturelles peut servir de guide général pour évaluer la condition écologique des paysages aménagés. Les approches qui utilisent l'ÉHV pour évaluer les paysages ont été basées sur les classes d'âge ou les stades de développement. Cela peut obscurcir la variation associée aux structures mortes et vivantes des peuplements. Le développement de l'ÉHV des caractéristiques structurales des peuplements pourrait améliorer la résolution écologique de cette approche du filtre brut pour évaluer les écosystèmes. Nous avons étudié l'ÉHV des biomasses vivante et morte dans le paysage régional de la chaîne côtière en Oregon en intégrant des modèles de biomasse à l'échelle du peuplement et un modèle spatialement explicite de simulation du feu. Nous avons simulé les paysages passés de la région pendant 1000 ans alors qu'ils étaient soumis aux régimes des feux qui ont précédé la colonisation euro-américaine et nous avons calculé la biomasse en fonction de l'historique des perturbations. La simulation a montré que les biomasses ligneuses morte et vivante ont énormément varié dans le passé, dans le temps et dans l'espace. Historiquement, la majorité des forêts contenaient 500–700 Mg·ha^{-1} (50–70 kg·m^{-2}) de bois vivant et 50–200 Mg·ha^{-1} (5–20 kg·m^{-2}) de bois mort. Les distributions actuelles des deux types de biomasse sont davantage concentrées en quantités beaucoup plus faibles. Bien que la restauration de l'ÉHV de la structure de la forêt ne soit pas nécessairement un objectif d'aménagement pour la plupart des propriétaires et des organismes d'aménagement, l'écart par rapport aux conditions de référence peut fournir une mesure relative pour évaluer la condition de l'habitat pour les aménagistes qui cherchent à utiliser la structure de la forêt comme moyen pour maintenir ou restaurer l'écosystème et la diversité des espèces.

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Introduction

The historical range of variability (HRV) in landscape and forest structure can serve as a "coarse-filter" (Hunter et al. 1988) reference to help guide biodiversity conservation and forest ecosystem management (Swanson et al. 1994; Landres et al. 1999). HRV has been defined as the bounded variability of characteristics of ecosystems within the constraints of larger-scale phenomena (e.g., climate and topography) and without significant modern human influence (Morgan et al. 1994; Landres et al. 1999). Previous studies have characterized the HRV in terms of landscape patterns of age-classes, developmental stages (e.g., open versus closed canopy), or dominant species (Wallin et al. 1996; Keane et al. 2002; Wimberly 2002). While these general metrics can provide valuable information about the ecological state of a for-

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ested landscape, they typically obscure variation in forest stand structure, which influences many ecological processes (Spies 1998). For example, stand age inadequately indicates the structure of live trees for uneven-aged stands and is a poor predictor of dead wood biomass in relatively young stands (Spies et al. 1988). Stand types and developmental stages can incorporate different fire histories to some degree (Keane et al. 2002), but it is difficult to characterize variation in amounts of dead wood on the basis of stand types and developmental stages because of the cumulative effects of historical disturbance events. Variation in forest structure can be more relevant than stand age-class in assessing changes in biodiversity because it can be more directly linked to habitat and ecosystem functions (Franklin et al. 1981; Hunter 1990; Spies 1998). Knowledge of the HRV of forest structural characteristics such as density, size distribution, spacing, diversity, and biomass of live and dead vegetation (Spies and Franklin 1991; Spies 1998) would provide managers with a larger set of dynamic reference conditions than they have now for evaluating the status and trends of forest ecosystems.

In this paper we characterize the HRV of two components of stand structure, live and dead stand biomass. Biomass of live and dead trees is a key attribute of forest ecosystems and can be sensitive to disturbance history and stand development (Harmon et al. 1990; Scheller and Mladenoff 2004). These structural metrics are directly related to ecological processes such as carbon sequestration and productivity (Turner et al. 1995) and closely related to habitat functions. For example, live biomass is probably closely related to vertical stand structure, which is known to influence microclimate and the habitats of many taxa (Brokaw and Lent 1999) Dead wood in the form of snags and logs plays many important roles in forest ecosystems including contributions to soil productivity and habitat diversity for vertebrates, invertebrates, and fungi and lichens (Harmon et al. 1986, Rose et al. 2000). In streams, large woody debris can contribute to habitat diversity for salmonids and other aquatic organisms (Harmon et al. 1986). The loss of large dead wood is considered one of the major ecological impacts of intensive forest management in this region (Spies and Cline 1988). Developing measures of HRV for stand structural features would advance our ability to evaluate the ecological effects of changes in forest dynamics that results from anthropogenic influences on forest ecosystems, such as timber harvesting, fire suppression, and climate change. We are aware of only one study that has quantified the HRV of dead wood biomass at the stand level (Tinker and Knight 2001) and none that have estimated the HRV of live or dead stand biomass at a landscape level.

The objectives of this simulation study are to (*i*) quantify the HRV in live and dead wood biomass and (*ii*) compare the biomass levels on the current and historical landscapes for the Oregon Coast Range. We expect that, based on previous stand-level studies, the biomass of dead wood currently found in the region is not within the HRV because of intensive forest harvesting in the last half century (Spies and Cline 1988). However, it is uncertain how stand biomass scales up to the entire region under the historical disturbance regime because the amount of wood biomass depends on stand disturbance history spanning many centuries.

Materials and methods

Study area

The Oregon Coast Range is a 2 × 10^6 ha physiographic province in Oregon (inset in Fig. 1). The climate is characterized by mild, wet winters and dry, cool summers, influenced by the Pacific Ocean to the west (Franklin and Dyrness 1988). As a result of orographic effects, the western half of the region has a moister climate than the eastern half. The topography is characterized by highly dissected mountains, steep slopes, and a high stream density. The soils are moderately deep to deep and fine to medium texture, derived from sandstone, shale, or basalt (Franklin and Dyrness 1988). Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco var. *menziesii*) is a long-lived seral dominant (Franklin et al. 2002). This species is fire-tolerant with thick bark that enables individuals to survive low- to moderate-severity fires (Agee 1993). Western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), a major shade-tolerant species, is dominant in young stands near the coast and late successional stands (>200 years) throughout the area (Spies and Franklin 1996; Franklin et al. 2002). Sitka spruce (*Picea sitchensis* (Bong.) Carrière) is the dominant species close to the coast (~5 km; Wimberly and Spies 2001), along with hemlock. Red alder (*Alnus rubra* Bong.) is a typical riparian species that can be abundant in disturbed areas.

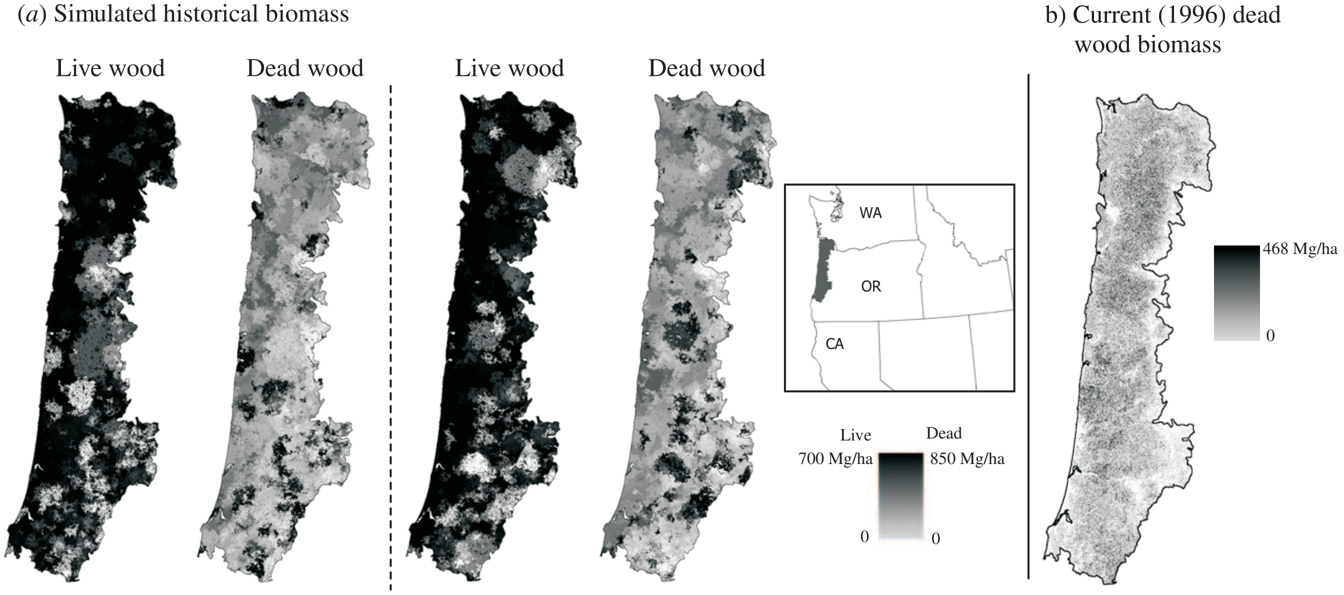
Large wildfires have been the most important historical disturbance shaping forests of the Oregon Coast Range (Agee 1993). The fire regime was relatively stable for the 1000 years prior to Euro-American settlement (Long et al. 1998). In presettlement time, the estimated mean fire-return interval ranged from 150 to 350 years for high-severity fires in this region (Long et al. 1998). Moderate-severity fires occurred often in mixture with high-severity fires (Impara 1997). High-severity fires often led to stand replacement, while moderate-severity fires left unburned forest patches and single trees, which can influence subsequent stand development (Weisberg 2004). Fires tend to be especially severe during the first 30 years of stand development when high amounts of flammable fuel remain after the previous fire (Agee and Huff 1987).

In the coastal valleys and the adjacent Willamette Valley, Native Americans set fires for agriculture and hunting (Boyd 1999). Some of these fires could have occasionally burned into the foothills of coastal mountains, but the evidence of this trend is not strong (Agee 1993; Whitlock and Knox 2002). The region experienced more frequent fire occurrences following Euro-American settlement in the mid-1800s (Weisberg and Swanson 2003), and high-severity fires were prevalent from the mid-1800s to mid-1900s. Effective fire suppression efforts began in the 1940s in western Oregon (Weisberg and Swanson 2003).

The general model of biomass dynamics

Our simulation model is based on the dead wood dynamics model of Harmon et al. (1986) and Spies et al. (1988), which characterizes the amount of dead wood as a sum of three major components: carryover from the prefire stand, dead wood created by fire, and mortality from the postfire stand. Live wood biomass is implicit in these models and is an essential companion for the dead wood model for calcu-

Fig. 1. (*a*) Examples of spatial patterns of live and dead wood biomass from the landscape age-class dynamics simulator (LADS) simulations for the Oregon Coast Range. Two sets from different time steps are presented here to illustrate the spatial and temporal variation in live and dead wood biomass. (*b*) The estimated distribution of dead wood biomass based on the model by Ohmann and Gregory (2002). Note the remarkable difference in spatial distribution of dead biomass between this map and simulated historical maps. The display color was stretched in gradations between the minimum and maximum values. The inset shows the location of the Oregon Coast Range in the Pacific Northwest of the United States.



(*a*) Simulated historical biomass

b) Current (1996) dead wood biomass

lating new inputs from mortality in the postfire stand. Our modeling approach only concerns two aggregate pools of biomass for live and dead wood and does not differentiate biomass pools by types such as sapwood, branches, or roots (e.g., Harmon and Marks 2002). The two pools represent structural components of forest stands and do not include soil organic matter. Fires affect dead wood biomass by causing tree mortality and by consuming wood (Agee 1993). A high proportion of fire-killed biomass enters the dead wood pool because fire consumption of green trees is relatively small (0%–10%; Agee 1993). Fire consumption of dead wood biomass from prefire mortality is estimated to range from 20% to 30% (Agee 1993), and this consumption is accounted for in carryover dead wood biomass.

In our model, the live and dead wood biomass of stands is a function of both fire severity and the interval between fires (Fig. 2). High-severity fires cause complete mortality of trees and convert live wood biomass into dead wood. Moderate-severity fires are assumed to be a mixture of crown and surface fires that can cause various degrees of mortality roughly ranging from 20% to 80%, partly depending on forest types and environmental conditions (Chappell and Agee 1996; Weisberg 2004). Because of uncertainty in parameterizing complex mortality patterns over a large region, we simply chose the midpoint (50%) of the range so that moderate-severity fires convert half of the live wood biomass to dead wood in our model. Immediately after a high-severity fire, dead wood legacies from the prefire stand are abundant. Live wood biomass increases with time as the stand develops, and dead wood biomass is the balance between input from postfire stands and loss from decay. Reburns, fires recurring within a few decades, can reduce live and dead wood biomass to very low levels.

Fig. 2. Conceptual model of the dynamics of live and dead wood biomass in response to different fire severities and frequencies in the Oregon Coast Range. The thick arrows are fire events, with the short ones being moderate-severity fires and the long ones high-severity fires. The dotted arrows indicate repeated burns, which return to the stand when live wood biomass has not been well developed. The thin arrows indicate stand development over time, and the length of the arrows indicates relative duration of intervals between fires. "Young with legacy" refers to young stands (<80 years) with high amounts of dead wood, and "young without legacy" refers to young stands with relatively small amounts of dead wood because of reburns. The shaded area conceptually indicates all possible ranges of pathways under the fire regime and forest growth. Mature, mature forests (80–200 years); OG, old-growth forests (>200 years).

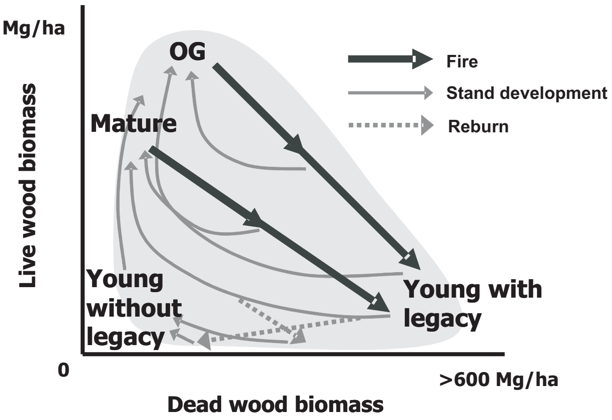


Table 1. Percent cover of the 36 combination classes of live and dead wood biomass in the Oregon Coast Range: (*a*) historical means and the 5th and 95th percentiles (parentheses) from model simulations, (*b*) estimated current condition, and (*c*) the difference between the current and the historical mean (values are in Mg·ha^{-1}).

(*a*) Historical mean (5th and 95th percentiles)

Live wood biomass levels	(Mg/ha)	0-50 Dvlow	51-100 Dlow	101-200 Dmed	201-400 Dmhigh	401-600 Dhigh	> 600 Dvhigh
		Dead wood biomass levels					
Lvhigh	>680	0	3.7 (2.7-4.8)	28.6 (19.7-36.4)	0	0	0
Lhigh	501-680	0	27.4 (20.1-36.7)	4.5 (3.1-6.2)	0	0	0
Lmhigh	351-500	1.9 (1.1-3.3)	7.6 (3.9-14.6)	3.2 (2.3-4.3)	3.7 (2.4-5.2)	0.5 (0.2-1.0)	0
Lmed	201-350	0.5 (0.2-1.0)	2.3 (1.1-4.2)	3.2 (1.6-6.6)	2.3 (1.6-3.0)	0.7 (0.3-1.3)	0
Llow	101-200	0.02 (0-0.05)	0.3 (0.1-0.7)	1.4 (0.7-2.7)	1.8 (0.6-4.4)	0.06 (0.02-0.1)	0
Lvlow	0-100	0	0.0 (0-0.1)	0.6 (0.2-1.5)	2.2 (0.9-4.8)	1.9 (0.6-4.4)	1.7 (0.6-4.2)

(*b*) Current condition

Live wood biomass levels	(Mg/ha)	0-50 Dvlow	51-100 Dlow	101-200 Dmed	201-400 Dmhigh	401-600 Dhigh	> 600 Dvhigh
		Dead wood biomass levels					
Lvhigh	>680	0.09	0.6	0.4	0.06	0.27	0
Lhigh	501-680	1.4	0.7	1.0	0.06	0.04	0
Lmhigh	351-500	2.7	2.1	2.4	0.8	0	0
Lmed	201-350	9.1	4.2	3.5	0.9	0	0
Llow	101-200	18.8	6.3	3.7	1.1	0	0
Lvlow	0-100	25.3	10.3	3.9	0	0	0

(*c*) Difference (current condition - historical mean)

Live wood biomass levels	(Mg/ha)	0-50 Dvlow	51-100 Dlow	101-200 Dmed	201-400 Dmhigh	401-600 Dhigh	> 600 Dvhigh
		Dead wood biomass levels					
Lvhigh	>680	0.09	-3.1	-28.2	0.06	0.27	0
Lhigh	501-680	1.4	-26.7	-3.5	0.06	0.04	0
Lmhigh	351-500	0.8	-5.5	-0.8	-2.9	-0.5	0
Lmed	201-350	8.6	1.9	0.3	-1.4	-0.7	0
Llow	101-200	18.8	6.0	2.3	-0.7	-0.06	0
Lvlow	0-100	25.3	10.3	3.3	-2.2	-1.9	-1.7

▓ Increased on the current landscape
░ Decreased on the current landscape
0 No difference

Abbreviations:

Live wood biomass levels		Dead wood biomass levels	
Lvlow:	very low	Dvlow:	very low
Llow:	low	Dlow:	low
Lmed:	medium	Dmed:	medium
Lmhigh:	medium high	Dmhigh:	medium high
Lhigh:	high	Dhigh:	high
Lvhigh:	very high	Dvhigh:	very high

Although only a few pathways are illustrated in Fig. 2, almost any pathways approximately within the shaded area are theoretically possible. The shaded area can be considered the HRV of stand biomass dynamics. The actual shape of the possible range depends on disturbance regimes and the rate of tree establishment and growth.

The simulation model and model parameterization

Historical landscapes were simulated by using the landscape age-class dynamics simulator (LADS), version 3.1 (Wimberly 2002). LADS is a spatially explicit, stochastic cellular-automata model designed to simulate forest landscape dynamics under fire regimes specified by the user. We applied this model to ask how stand live and dead wood biomass in the Oregon Coast Range varied historically. We constructed the HRV of biomass dynamics from the Monte Carlo simulations in LADS. LADS simulates fire patterns based on the probabilities of fire ignition, spread, and extinction, which vary with topography, wind, and fuel accumulation inferred from time since fire. LADS neither simulates the physical processes or behavior of fire nor directly models fuel accumulation. It simulates the spatial pattern of fires probabilistically using stochastic functions and fire susceptibility of cells. Fire susceptibility is assigned to each cell as a function of climate, topography, stand age (as a surrogate for fuel loading), and wind direction and speed (Wimberly 2002). Relatively infrequent, high to moderate severity fires are characteristic to the moist forests of the Oregon Coast Range, and under extreme conditions (i.e., low fuel moisture and high wind speed) where such fires can occur, various types of forests tend to become equally flammable and depend less on fuel load but more on climatic and weather variables (Bessie and Johnson 1995). Given the characteristics of the fire regimes in the region, we think that it is not necessary to mechanistically model fuel accumulation, especially fine fuels, for our objectives. LADS uses time since fire as a surrogate for fuel loading, following the model proposed by Agee and Huff (1987) for western Pacific Northwest forests.

Efficiency in computation for simulating over a large area over a long time period was achieved by using a coarse-grained representation of the landscape, which also reduced the number of input parameters. The landscape of the Oregon Coast Range was represented in LADS as a grid of 9 ha cells (300 m × 300 m). Wimberly (2002) parameterized LADS to the historical fire regimes prior to Euro-American settlement around the mid-1800s using dendrochronological data collected in the central part of the province (Impara 1997) aided by paleoecological data from lake sediment cores (Long et al. 1998). The fire-spread algorithm was validated by comparing simulated fire shape and size with data from actual fires and by examining the proportion of unburned interior forest "islands" within larger burns (Wimberly 2002). Simulations yielded fire patterns that well captured the aggregated, statistical characteristics of actual fires (Wimberly 2002). This type of model validation is appropriate for probabilistic spatial models and considered rigorous (Turner et al. 1989). Because of the coarse representation, fine-scale heterogeneity such as canopy gaps and fire breaks cannot be inferred from the model outputs. The simulation requires quantitative data on the fire regime, natural fire rotation, size and shape distributions of burned patches, and the effects of slope position, vegetation age, and wind on the direction and probabilities of fire ignition and spread.

To reflect variability in fire and uncertainty in the data, the frequency, severity, and size of fires were modeled as random variables drawn from probability distributions estimated from data (see Wimberly 2002 for details). The probabilities of fire ignition in randomly selected initiation cells and the spread of fire from adjacent cells increased with elevation and fuel availability. Previous fire studies in the western Pacific Northwest suggest that susceptibility to fire increases with elevation and that fuel loads are high in early and late successional stages (Agee and Huff 1987). Shapes of fires were calibrated to match the boundaries of fire events shown on historical fire maps and satellite images of areas with known fire history. The landscape was subdivided into two climate zones, coastal (northwestern two-thirds) and interior (southeastern one-third) (Wimberly 2002). The coastal zone is moist and characterized by a longer natural fire rotation (NFR), while the interior zone is dryer and was historically more frequently burned (Impara 1997). Fires were likely to be larger and more severe in the coastal zone than in the interior because of greater fuel accumulation and less frequent occurrence of climatic conditions favoring fire (Agee 1993). Because simulated fires spread stochastically from cell to cell as a function of cells' fire susceptibility, unburned or partially burned forest islands are often left behind within larger burns.

We modified the LADS for this study to simulate live and dead wood biomass dynamics in each cell as a function of time since last fire and fire severity. Fire severity determines the level of mortality in live wood, while time since last fire is used to compute decay in dead wood and growth in live wood. The components in the model were live and dead wood pools, fire and chronic mortality of trees, decay, and fire consumption of wood. Chronic mortality is defined in this model as tree death from causes other than fire (e.g., self-thinning, disease and (or) pathogen). Net live wood biomass at time step t (LBB_t) in a stand (in $\mathrm{Mg \cdot ha^{-1}}$; $1\ \mathrm{Mg \cdot ha^{-1}} = 0.1\ \mathrm{kg \cdot m^{-2}}$) was modeled as a Chapman–Richards function (Richards 1959)

$$[1] \qquad \mathrm{LBB}_t = a\left\{1 - e^{[-b(\mathrm{BIOAGE}_{t-1}+\mathrm{STEP})]}\right\}^c$$

where parameter a (see the list of parameters in the Appendix A) is the asymptote of the curve and indicates the maximum possible stand biomass, b controls rates, and c controls time lag for a stand to reach the maximum biomass. STEP is the simulation step length in years. Although the model runs on a 10 year time step, a given cell can burn more than once within a time step (outputs summarize decadal fire occurrences). Biomass age (BIOAGE_t) was calculated from the amount of live wood biomass left in the stands after a fire event at time t ($\mathrm{LBB}_{t(\mathrm{f})}$, where $t(\mathrm{f})$ indicates the occurrence of a fire at time t)

$$[2] \qquad \mathrm{BIOAGE}_t = \frac{\log\left(1 - \sqrt[c]{\frac{\mathrm{LBB}_{t(\mathrm{f})}}{a}}\right)}{-b}$$

$$[3] \qquad \mathrm{LBB}_{t(f)} = (1 - \mathrm{FMORT})\mathrm{LBB}_t$$

Table 2. Results from sensitivity analyses of landscape age-class dynamics simulator (LADS) model simulations of historical Coast Range

Biomass levels			P_a		P_b		P_c		CMORT	
Live wood	Dead wood	Baseline	+	–	+	–	+	–	+	–
Lmed	Dlow	2.3	–0.5	2.2	–0.4	2.8	0.8	–0.2	–0.5	–0.1
Lmed	Dmed	3.2	–0.3	–0.4	0.3	–1.1	–1.7	0.4	0.1	0.3
Lmed	Dmhigh	2.3	–0.8	2.1	–0.4	0.1	–0.1	0.1	0.4	0.2
Lmhigh	Dlow	7.5	–4.5	9.0	–3.5	–0.6	–3.2	–2.2	0.2	–1.5
Lmhigh	Dmed	3.2	–1.6	0.9	–1.3	0.8	0.1	–0.2	0.6	0.5
Lmhigh	Dmhigh	3.7	–0.8	–3.0	0.3	–0.8	–0.2	0.0	0.7	–0.8
Lhigh	Dlow	27.4	–17.3	4.5	–2.0	1.0	0.3	0.8	–11.9	2.0
Lhigh	Dmed	4.5	0.9	10.4	2.2	1.1	0.1	1.2	12.2	–2.6
Lvhigh	Dlow	3.7	6.2	–3.7	2.2	–2.3	–0.3	0.5	0.5	12.7
Lvhigh	Dmed	28.6	11.9	–28.6	4.2	–5.0	–0.3	0.8	–1.5	–13.8
Total changes in the other 26 classes		13.6	6.9	6.6	–1.6	4.0	4.5	–1.3	–0.8	3.1

Note: The values are percents of the area in the region (% landscape). The baseline column contains the mean values from the simulations with original The columns with + and – contain the results from analyses with higher and lower parameter values tested for the respective parameters. Only the 10 most parameter *a*; P_b, Chapman–Richards parameter *b*; P_c, Chapman–Richards parameter *c*; CMORT, chronic mortality; CONS, dead wood consumption by fire; NFR, natural fire rotation; and SEV, severity of fires. Abbreviations for live-wood biomass levels: Lvlow, very low; Llow, low; Lmed, medium; Lmhigh, Dmhigh, medium high; Dhigh, high; and Dvhigh, very high.

where FMORT is the proportion of live wood biomass killed by fire at time *t* (set at 1.0 for high-severity fires and 0.5 for moderate-severity fires). If fire did not occur, BIOAGE was incremented simply by 10 years (one time step). Because BIOAGE is purely a function of live wood biomass and not an actual stand age, live wood biomass calculated by this equation was independent of time since stand replacement (i.e., stand age). This scheme allowed live wood biomass to increase proportionally to standing biomass (Grier and Logan 1977; Acker et al. 2002; Scheller and Mladenoff 2004). The live wood biomass curve was calibrated by using existing chronosequence field data from 42 sites in the southern Coast Range ranging in age from 40 to about 525 years[3]; biomass peaked at around 700 Mg·ha^{-1} by 250 years of age and stayed fairly level through 500 years. This biomass–age pattern is in accordance with previous studies (Greene et al. 1992, Acker et al. 2000, 2002, Janisch and Harmon 2002). We selected values of the parameters (a = 700, b = 0.02, and c = 1.5) to capture this general pattern of biomass accumulation.

The dead wood biomass at time step *t* (DWM_t) was computed as follows

$$[4]\qquad \mathrm{DWM}_t = \{\mathrm{DWM}_{t-1}[e^{(\mathrm{DECAY}\times\mathrm{STEP})}] + \mathrm{CMORT} \times \mathrm{LBB}_t\}(1 - \mathrm{CONS}) + \mathrm{LBB}_t \times \mathrm{FMORT}$$

where DECAY is the decay and fragmentation rate per year, CMORT is the chronic mortality rate per time step in percent of biomass, and CONS is the rate of fire consumption of carryover dead wood from before the fire. Because fires in this region are often rapidly moving (i.e., extreme conditions), most of the dead wood consumption by fire presumably comes from dead wood in advanced decay stages. Highly decayed components comprise about 25% of the total dead wood biomass present in these forests (Spies et al. 1988). We thus assumed fire consumption of carryover dead wood to be 25% for either high- or moderate-severity fires, which agrees with previous empirical and modeling studies in the Pacific Northwest forests (Fahnestock and Agee 1983; Wright et al. 2002). We assumed that fire does not consume newly killed biomass (Agee 1993). In the case of no fire occurrence, CONS and FMORT were set to be zero.

DECAY and CMORT can vary in the model with time since the last fire (Appendix A). CMORT was zero for stands <30 years old because dying trees are assumed to be too small to be recruited as coarse woody debris since they are the smallest suppressed classes (Franklin and DeBell 1988; Wright et al. 2002). For stands >30 years old, CMORT was fixed at 0.5%/year (Harcombe et al. 1990; Greene et al. 1992; Acker et al. 2000, 2002). CMORT was increased for the first 50 years after moderate-severity fires to reflect elevated mortality due to delayed mortality from fire injury (Spies et al. 1988).

DECAY was set based on literature and expert knowledge (Harmon et al. 1986; Spies et al. 1988; Janisch et al. 2006; M. Harmon (2003, personal communication and unpublished data)); its value reflected distributions in size, form (snag or log), and species composition across age-classes in Pacific Northwest forests. Decay rates are lower for larger pieces and remarkably lower for early-successional Douglas-fir than for late-successional western hemlock (Graham 1982; Harmon et al. 1986; Stone et al. 1998; M. Harmon (2003, unpublished data)). Fragmentation rates are considerably higher for snags than for logs, and DECAY in the early stages of forest development was elevated because most dead trees are standing following fires (Agee and Huff 1987; Spies and Cline 1988; Spies et al. 1988). The accumulation of dead wood from postfire stands peaks in the old-growth stage followed by gradual decline to a lower equilibrium as a result of shifts in species dominance from Douglas-fir to western

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[3] T.A. Spies, J.F. Franklin, G. Spycher, and R. Pabst. Aboveground biomass and carbon storage in natural Douglas-fir stands in relation to stand and site characteristics in western Oregon and Washington. *In* Carbon dynamics of two forest regions: northwestern Russia and the Pacific Northwest. In preparation.

landscapes.

CONS		DECAY		FMORT$_h$		FMORT$_m$		MFS		NFR		SEV	
+	–	+	–	+	–	+	–	+	–	+	–	+	–
–0.2	–0.4	0.8	–1.1	–0.1	–0.6	0.0	–0.1	–0.3	–0.2	–0.3	0.2	0.4	–0.4
–0.2	0.0	–0.9	0.6	0.0	–0.1	0.0	0.0	–0.4	0.2	–0.5	0.7	0.3	–0.4
0.2	–0.1	–0.2	1.0	–0.1	1.0	–0.2	–0.6	–0.2	0.1	–0.4	0.6	–0.4	0.4
–0.6	–0.3	–1.6	–1.3	–1.1	–2.3	0.4	–0.3	0.2	–1.3	–0.9	0.1	1.6	–1.3
0.1	–0.1	0.6	1.4	0.2	0.9	0.0	–0.8	–0.1	0.4	–0.4	0.6	–0.2	0.5
0.1	0.3	–1.1	1.1	0.0	0.4	–0.5	0.9	0.0	0.2	–0.1	0.0	–0.7	0.9
0.1	0.2	3.4	–10.1	2.5	2.4	0.3	–0.3	0.5	–0.2	–0.6	2.2	1.2	–0.1
–0.2	0.0	–3.0	–4.1	0.7	0.1	–0.7	1.5	0.2	0.4	–0.2	0.0	–0.7	0.8
0.1	0.0	9.6	–3.7	0.2	0.1	–0.3	0.3	0.0	0.1	0.8	–1.0	–0.2	0.3
0.5	–0.5	–10.1	–2.9	0.0	1.3	0.5	0.9	1.1	0.6	5.2	–5.8	–1.9	0.7
0.1	0.7	2.5	19.2	–2.2	–3.3	0.5	–1.6	–0.8	–0.5	–2.7	2.4	0.6	–1.1

parameter values. The results are reported as difference from the baseline mean in % landscape. The parameters examined are in the first row. abundant classes were analyzed, and aggregated changes in the other minor classes are reported in the bottom row. P_a, Chapman–Richards DECAY, decay rates for dead wood; FMORT$_h$, high-severity fire mortality; FMORT$_m$, moderate-severity fire mortality; MFS, mean fire size; medium high; Lhigh, high; and Lvhigh, very high. Abbreviations for dead-wood biomass levels: Dvlow, very low; Dlow, low; Dmed, medium;

hemlock, which has smaller diameters and faster decay rates (Harmon et al. 1986). DECAY was increased for the interior zone by 25% because the environment is more favorable for decay in the drier, warmer interior zone than in the wet coastal zone. High moisture and cooler summers near the coast can slow the decay process and microbial activities in coarse woody debris (Progar et al. 2000).

Model simulation and data analysis

We used one hundred 1000 year simulation runs and obtained summary outputs that integrate fire occurrences for every 10 year step. Numerous simulation runs were necessary to represent the full range of possible fire patterns from stochastic models (Wimberly 2002). To exclude the transient dynamics from the analysis, we ran the model for 2000 years and discarded the first 1000 years of the simulations. The 1000 year simulation length was an appropriate time scale to capture variations in Coast Range forests because 1000 years is the approximate longevity of dominant Douglas-fir trees in the region and is several times the length of the mean fire return interval (Wimberly 2002). We randomly selected one map from each 1000 year run to ensure statistical independence (a total of 100 maps). We used ArcGIS Arc 8.3 (ESRI Environmental Systems Research Institute, Inc., Redlands, California) to process the outputs.

From the model outputs, we characterized the HRV of live and dead wood biomass in terms of the area covered with different amounts of biomass. We grouped the amounts of live and dead wood biomass into six levels and calculated the percentage of area in the region occupied by the 36 (6 × 6) biomass combination classes (Table 1*a*). Categorizing the variation in biomass into six levels inevitably reduced information content in the data set, but it was necessary for summarizing the results succinctly. The six levels were chosen to be fine enough to resolve characteristic amounts of biomass after different types of fire but not to overwhelm the interpretation. We then examined the percentage of area occupied by the six dead wood levels by major stand age-classes or stages recognized in the region (Spies and Franklin 1996; Franklin et al. 2002): (1) very open (0–10 years), (2) patchy open (11–20 years), (3) young (21–80 years), (4) mature (81–200 years), and (5) old growth (>200 years). We considered the 5th–95th percentile ranges as the bounds for the HRV of the area occupied by each biomass level.

We compared the current levels of live and dead wood biomass in the study area with the HRV. The current biomass map for the Oregon Coast Range was derived from the model developed by Ohmann and Gregory (2002), which is a statistical model based on satellite images, inventory plots, and GIS layers. Biomass was calculated from dimensions of wood in the plot data weighted by species specific gravity and, for dead wood, a decay class reduction factor. The correspondence of the map with the plot data was excellent ($r^2 > 0.99$) with respect to class area of the 36 live and dead wood combined classes (see model verification in Ohmann and Gregory 2002). Because only one modeled map was available for the current conditions, we were not able to quantify the uncertainty around the estimates.

Sensitivity analysis

We examined sensitivity of model outputs to changes in the input parameter values as changes in the percentage of the landscapes occupied by the live and dead wood biomass levels. Most of the parameter values varied by ±20% from the baseline values (Table A1). For some parameters, values within a reasonable range were selected to examine the effects. Sets of parameter values were altered one at a time, and changes were expressed as absolute difference from the baseline mean area. Standard deviation of fire size (SDFS) and mean fire size (MFS; Table A1) were varied simultaneously because fire size and its standard deviation are often highly correlated on real landscapes (Wimberly 2002). The SEV (fire severity) parameters were varied simultaneously so that the proportions of high-severity fires in each size-class were collectively varied by 20% (Wimberly 2002). The DECAY and CMORT parameters were also varied simultaneously across the age-classes. We conducted 10 independent 1000 year simulation runs and obtained summary output at 10 year intervals for each parameter set. We examined sensitivity for the 10 most abundant classes, which comprised 86.4% of the mean area for the baseline runs.

Results

Historical live and dead wood biomass in the Oregon Coast Range

The model simulations showed that spatial distributions of live and dead wood biomass are characterized by various sizes and shapes of overlapping patches with very low to very high biomass levels (Fig. 1). The distributions of the two kinds of biomass at the regional scale were almost mirror images of each other, with low live wood biomass corresponding to high dead wood biomass. Landscape patterns of live and dead wood biomass differed among time steps; patches with various levels of biomass shift over the landscape, changing size and shape. This indicates high spatiotemporal variability in the distribution of biomass in the historical landscape of the region.

Expressed in terms of area, two live–dead wood biomass combination classes were far more abundant than the other classes (Table 1*a*). The most abundant class was Lvhigh–Dmed, which occupied about 29% of the region (Lvhigh, live wood biomass very high; and Dmed, dead wood biomass medium; the biomass combination classes will be expressed as “live wood biomass class – dead wood biomass class”, and the first letter, L or D, denotes live and dead wood biomass, respectively. See Table 1 for abbreviations of the biomass classes). The second most abundant class was Lhigh–Dlow, which covered about 27%. Twelve classes, mostly the combinations of high live and dead wood biomass, did not occur in the simulated landscapes. Forests with very high dead wood biomass (Dvhigh) occurred only in combination with very low live wood biomass (Lvlow). On average, >80% of the historical landscapes were in low to medium dead wood levels (Dlow to Dmed; Fig. 3). Separate analyses for the two climate zones showed that amounts of dead wood were less in the interior than in the coastal zone (results not shown). Dvlow (dead wood very low) was more common in the interior (mean = 6.2%) than in the coastal (mean = 0.2%). About 53% of the coastal zone was in the Dmed level, while 57% of the interior was in the Dlow level.

As expected, the current landscape contained lower levels of both live and dead wood biomass than the historical landscapes (Fig. 3). The two historically most abundant classes, Lvhigh–Dmed and Lhigh–Dlow, were currently close to nil (Tables 1*b* and 1*c*). Forests with Lvlow–Dvlow occupied more than 25% of the current landscape, although the modeled outputs suggest that they were historically very rare. All the dead wood classes were outside the HRV in the current landscape in terms of area covered (Fig. 3). Forests in the Dvlow level occupied about 57% of the current landscape, compared with 2.5% under the historical regime. Dlow and Dmed levels were particularly reduced from their historical levels. The areas covered by Dmhigh, Dhigh, and Dvhigh levels were slightly lower than the historical levels.

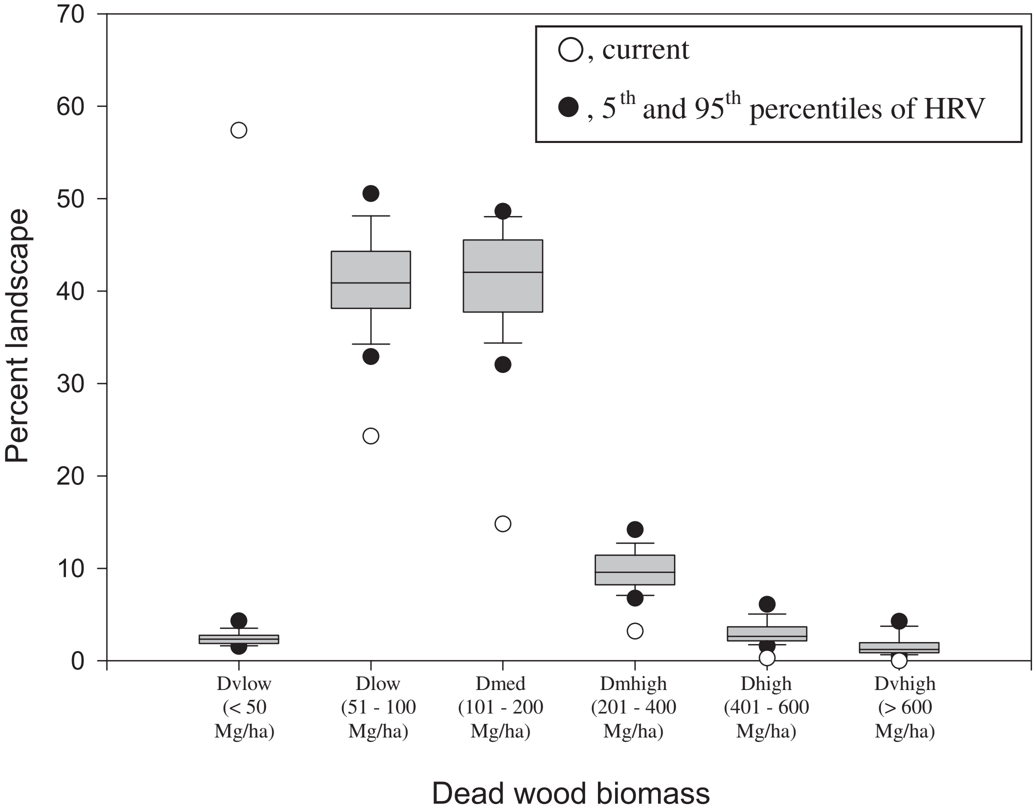
The historical distributions of dead wood biomass levels differed among age-classes (Fig. 4). Within each age-class, there were variations both in dead wood biomass and in area occupied by the six dead wood levels. Higher amounts of dead wood were typical of the very open and patchy open stages. Lower dead wood levels became more common in young and mature stages, with about 80% of the mature stage containing low amounts of dead wood. Dmed increased in the old-growth stage. Dvlow did not historically occur in very open, mature, and old-growth stages. Dvhigh occurred only in the very open stage. The patchy open and young stages also contained Dvlow, but such conditions were rare (Table 1*a*). The general trends of the current dead wood biomass by age-class indicated that stands with Dvlow were more abundant than the HRV in the current landscape for all the age-classes (Fig. 4). The old-growth stage showed a different trend across the dead wood classes with greater current areal coverage of higher amounts of dead wood (Dmhigh and Dhigh). The estimate of current conditions for the old-growth stage should be viewed with caution, however, because only a few inventory plots fell into this currently rare stage.

Sensitivity analysis

The change in the mean percentage of area in the region for the 10 most abundant biomass classes varied somewhat among parameters and biomass levels, but the majority of the differences were less than 3% (Table 2). The largest change was a reduction in the Lvhigh–Dmed class by 28.6% associated with Chapman–Richards parameter *a* (P_a), which caused the disappearance of the class. Another notable change was that 19.2% of the area was shifted into the minor 26 classes, causing the total area covered by these classes to increase from 13.6% to 32.8%. Despite these changes, the overall trend in the distribution of biomass classes did not change substantially from the baseline run, and the changes were due to shifts between neighboring classes (Fig. 5). The largest reduction was compensated for by an increase in Lhigh–Dmed and Lmhigh–Dlow (Table 2), so that the landscape condition still stayed outside the HRV. In their sensitivity analysis, Scheller and Mladenoff (2004) reported a much smaller change for the biomass module of LANDIS. However, they examined percentage change in the mean biomass for the entire simulated landscape, which should be considerably more robust to changes in input parameter values than the metric we used. Because we are interested in areal coverage of the biomass classes, we used absolute difference in percent cover in area from baseline mean area by biomass class for sensitivity analysis.

The influential parameters in the tested ranges were Chapman–Richards parameter *a* (potential maximum live wood biomass), decay rates, chronic mortality rates, and to a lesser degree, Chapman-Richards parameter *b* (growth rate). These parameters had relatively large influences on the Lvhigh–Dmed and Lhigh–Dlow classes (Table 2). These influential parameters controlled the live wood biomass growth (Chapman–Richards parameters *a* and *b*) and input and output rates of the dead wood pool (chronic mortality and decay rates) in the model. Regardless of the changes in these input parameter values within the tested ranges, the current conditions of the two lowest and two highest live wood biomass levels (Lvlow, Llow, Lhigh, and Lvhigh) and three dead wood biomass levels (Dvlow, Dmed,

Fig. 3. The historical ranges of variability in percentage of landscape covered by different dead wood biomass levels based on 100 simulated landscapes. Current levels of dead wood distribution, ○. Box plots display the median (center line), 25% and 75% quantiles (box), 10% and 90% quantiles (whiskers), and 5% and 95% quantiles (●).



and Dmhigh) are consistently far from the HRV (Fig. 5). Less important within the tested range were Chapman–Richards parameter *c* (controls initial lag in the growth model) and the parameters for fire consumption of wood (CONS), fire mortality (FMORT), and fire regime (MFS, NFR, and SEV).

We also plotted the biomass values from the baseline simulations against stand age to qualitatively compare with the data from the forest inventory analysis plots (conducted by USDA Forest Service) with no harvest history and from old-growth plots of Spies and Franklin (1988). The purpose here is to check whether LADS generates comparable variation in stand biomass seen in the inventory data from numerous (~200) plots scattered across the Oregon Coast Range. The range of biomass values from the simulations reasonably matched that of the plot data except for a few plots that had unusually low dead wood biomass in the inventory data (data not shown).

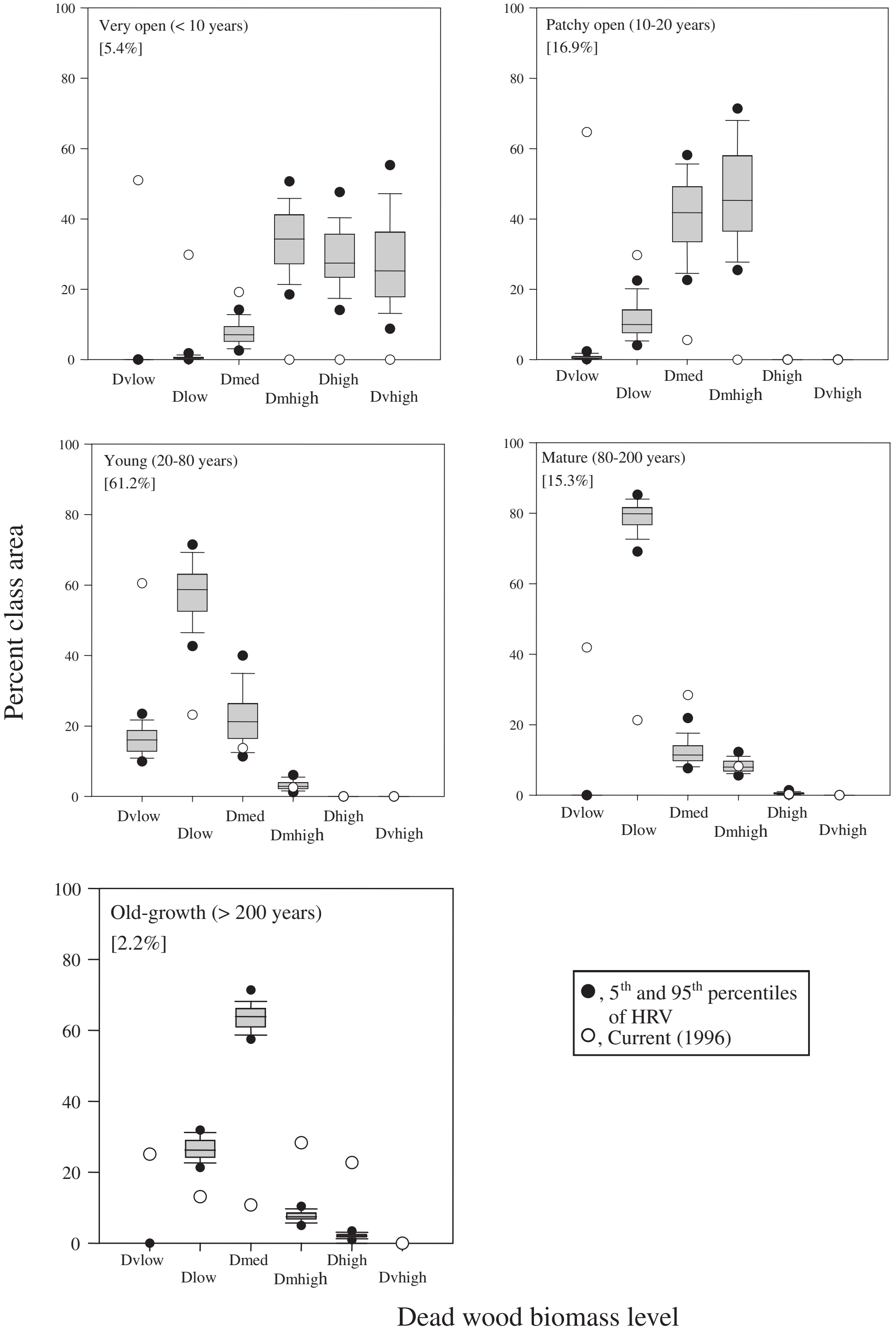
Discussion

Model limitations and assumptions

Fire is one of many factors that determine the distributions of biomass on a landscape. Other factors include site productivity, topography, wind, and environmental conditions for wood decay and fragmentation (Harmon et al. 1986; Spies et al. 1988; Scheller and Mladenoff 2004). However, fire history has an important influence on dead wood biomass in the Oregon Coast Range because infrequent stand-replacing fires create a large pulse of dead wood that persists for a long period of time owing to the large biomass and decay resistance of Douglas-fir. Therefore, we think that, although other potential factors are missing from our model, our approach is a reasonable first approximation to examine the dynamics of biomass in the study area.

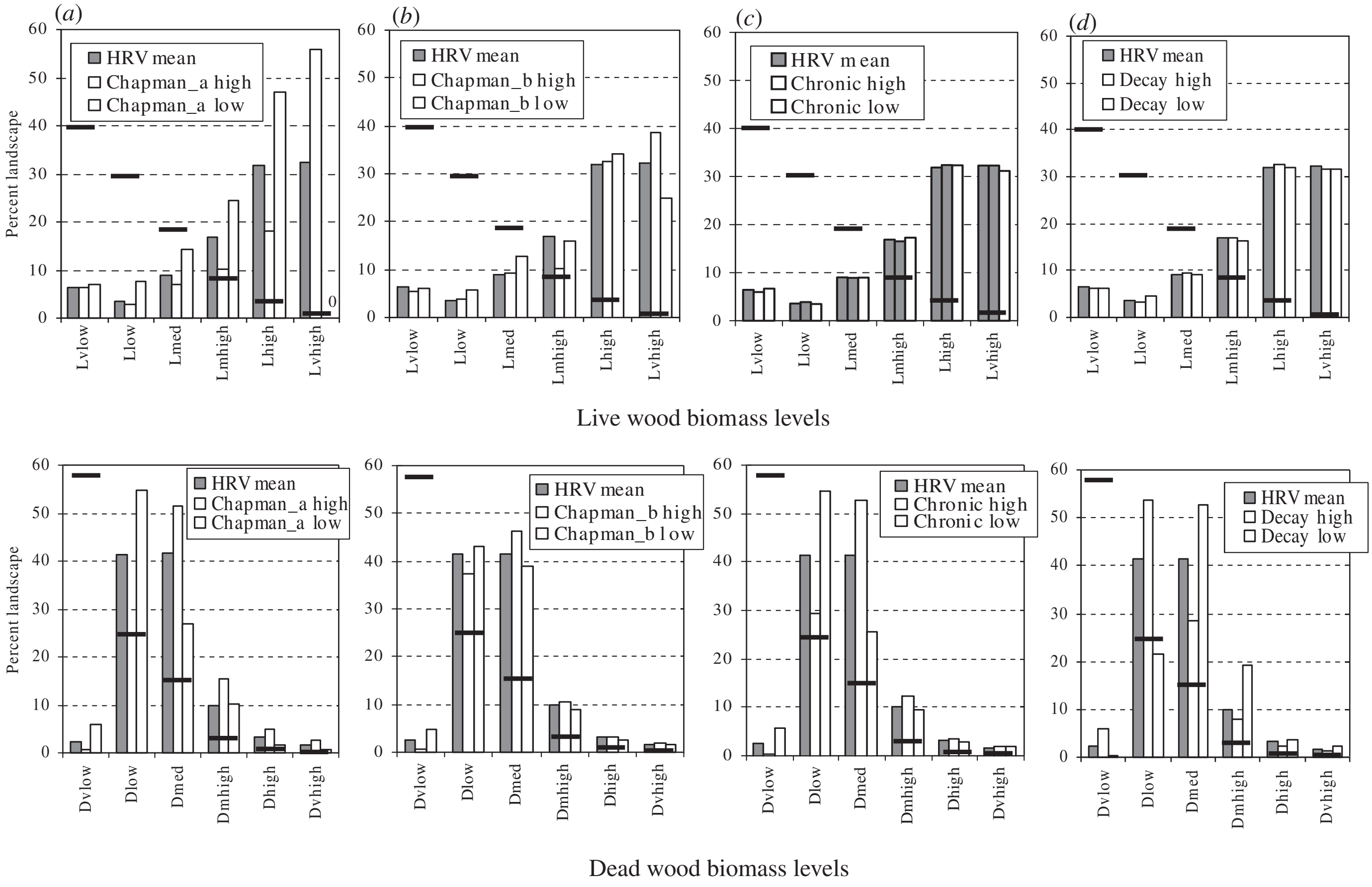
Our characterization of HRV may underestimate historical variation in the Coast Range because the model did not include multiple pathways of live and dead wood biomass dynamics, growth, mortality, decay, and fire consumption of wood, and these rates were deterministically assigned to cells, based on the state of cells. In other words, potential sources of variation that are specific to locations were not included in this model. The model used one equation to represent the live wood dynamics of the entire region, although there are many factors that could affect biomass growth in stands. Productivity, availability of seed source, and species present after fire are likely to influence the rate at which trees fill in stands and grow (Kashian et al. 2005). Yang et al. (2005) found multiple pathways of increase in canopy cover during early succession in the Coast Range. In some areas of the Pacific Northwest tree regeneration can require many decades to reoccupy a site (Franklin and Hemstrom 1981; Huff 1995). Our model used only one set of decay and mortality rates that varied with time since the most recent fire for each climate zone. Decay and mortality rates would change over time and across space in real landscapes, reflecting fluctuating site conditions (e.g., moisture and temperature) and varying mortality rates among locations and species (Muller 2003).

Fig. 4. The historical ranges of variability by age-class in percentage of landscape covered by different dead wood biomass levels. The numbers in brackets are percentages of current landscape in the age-class. For the interpretation of box plots, see Fig. 3.



The simulation results suggest the prevalence of very high live wood biomass levels (>500 Mg·ha^{-1}) on historical landscapes, especially when compared with those in the current landscape. This finding is reasonable if we assume that old forests were more prevalent historically. However, it could also suggest that the maximum live wood biomass parameter used in the Chapman–Richards function (Chapman parameter *a*) was too large. The productivity of forests on the eastern side of the Coast Range is less than that of forests on the western side, but for simplicity, the model used the same value for the maximum live wood biomass parameter as well as for growth rates for both areas. The effects of different forest productivity rates on HRV estimates need further investigation, but the sensitivity analysis indicates that the

Fig. 5. Results from the sensitivity analysis, displayed separately for live and dead wood biomass. Columns show results from the analysis that tested the same parameter. (*a*) Chapman–Richards parameter *a*, (*b*) Chapman–Richards parameter *b*, (*c*) chronic mortality rate, and (*d*) decay rate. Only the results from the most influential parameters are shown. The horizontal bars indicate the estimated current levels of biomass.



overall distribution of dead wood biomass was reasonably robust with regard to the input parameters within the tested range despite the apparently greater differences in live wood biomass. Notably, the area covered with low and moderate levels of dead wood biomass (Dlow and Dmed) was about 80% for all three input values of Chapman–Richards parameter *a*. Therefore, we think that the HRV estimates of dead wood biomass distribution are robust enough to use as an approximation of HRV, albeit a lower bound.

Sensitivity analysis indicated that chronic mortality and decay rates were influential factors in the model, and therefore, accurate estimates of the rates are desirable. Scheller and Mladenoff (2004) also found that the decomposition rate was influential for their dead wood model. Our model assumed relatively large decay and (or) fragmentation rates early in stand development to reflect abundant snags after fire and small trees dying from suppression, but large pieces of legacy wood could substantially decrease overall decay rates. Weighting decay and (or) fragmentation rates by the proportions of snags and species and by size distribution of dead wood will improve the estimation. Stand density affects density-dependent mortality, especially in young stands (Kashian et al. 2005), but the variation in stand density was not considered in this model. Stand density may be affected by many factors such as seed availability and edaphic conditions, but the structure of LADS could not easily incorporate these factors. Incorporating the variation in tree density among young stands would improve the model if data are available for parameterization because the variation tends to be greater in young stands than old stands where tree density may converge (Kashian et al. 2005). Since our sensitivity analysis was not a full factorial analysis, we cannot infer any possible interaction effects of combinations of the parameters (other than the ones we tested). However, considering the computation time for such an analysis and correlation among parameters, our analysis provides a useful initial characterization of the behavior of the model with respect to changes in input parameter values.

The HRV and current distribution of live and dead wood biomass

The simulations indicated that historical landscapes of the Oregon Coast Range contained a wide variety of combinations of live and dead wood biomass. The most abundant biomass classes corresponded to mature and old-growth forests with their characteristic amounts of dead wood. The overall pattern of the distribution was somewhat expected based on previous studies, which suggested that 50%–70% of the region was covered with mature or old-growth forests (Wimberly et al. 2000, 2004; Wimberly 2002; Nonaka and Spies 2005). We also expected low coverage of high to very high dead wood (Dhigh and Dvhigh) because this type of structure is only associated with conditions shortly after a high-severity fire in mature or old-growth forests. In contrast, although reburns were expected, it was not clear how much they influenced the overall biomass distribution. Similarly, uncertain was the relative influence of moderate-severity fires on dead wood amounts in young and mature forests. Moderate-severity fires were important for the abundance of classes with moderate to high live and dead biomass (Lhigh–Dlow and Lvhigh–Dmed).

Very low dead wood conditions (Dvlow) occurred in the simulated landscapes, with the amount sometimes as low as that observed in young plantation forests. Spies and Cline (1988) reported that intensive plantations in the Pacific Northwest may contain only 20–40 Mg·ha^{-1} of dead wood. As the model suggests, reburns created very low dead wood conditions in the historical landscapes. Such conditions were associated with low to moderately high levels of live wood biomass (Llow, Lmed, and Lmhigh), approximating very young to young forests (10–80 years). However, at the regional scale, we found that stands with very low dead wood levels were not historically common, covering only 2.5% of the region. Therefore, the levels found in young plantations in the current landscape are within the HRV at the stand scale but outside the HRV at the regional scale.

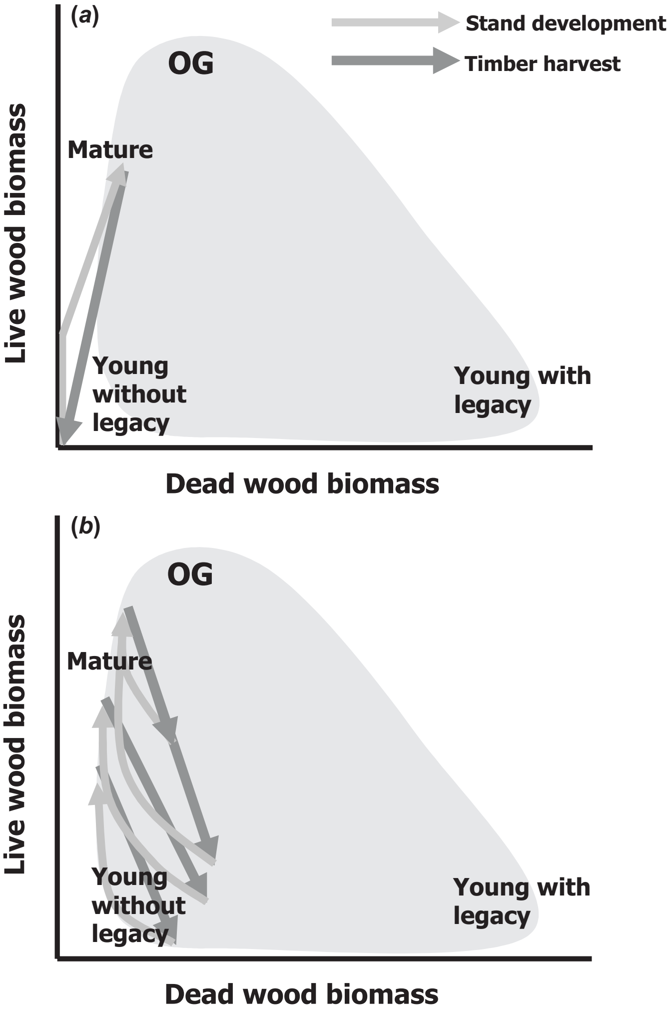
Dead wood biomass in stands across age-classes varied widely around the general U-shape trajectory (Spies and Franklin 1988). The variation arose from variation in fire histories (Spies et al. 1988) and partially from climatic differences between the two zones. Different fire histories lead to different amounts of legacy wood as well as to variation in the peak magnitude for dead wood input from each fire. Fire history effects are larger in younger stands because, according to the model, most legacy wood becomes insignificant in the dead wood pool by about 100 years, and mortality from the developing stands becomes more important in later seral stages. The climatic difference was also important because 97% of the area with dead wood <50 Mg·ha^{-1} occurred in the interior zone, where wood decays faster and reburns were more common.

The large area with low levels of both live and dead wood biomass (Lvlow–Dvlow) on the current landscape is probably a result of the frequent wildfires during the mid-1800s and timber harvesting since the mid-1940s, especially clearcutting. Timber harvesting results in reduced dead biomass inputs from disturbance (Tinker and Knight 2001).

Management implications

On the current landscape of the Oregon Coast Range, forest management, in addition to wildfire, is an important agent of disturbance. This study showed that forest structure in terms of live and dead wood biomass is largely a function of stand-disturbance histories. Anthropogenic disturbances can drive trajectories of forest dynamics differently from natural disturbances. How much "space" of the HRV of forest dynamics (i.e., the shaded area in Fig. 2) occupied by trajectories driven by forest management can provide coarse measure to assess management effects on the variation of forest structure with respect to the HRV? For example, short rotations (<40 years) prevent stands from accumulating large live wood biomass. The dynamics of live and dead wood biomass under intensive forest management may fall outside the HRV (Fig. 6*a*), so that management probably creates forest structure mostly outside HRV. Retaining live and dead trees after harvest for greater structural diversity could lead to conditions within the HRV, but young stands with lots of legacy wood would be still rare (Fig. 6*b*). If desired future conditions could not be reached by trajectories under current management regimes, either the management goal or regimes may need to be reframed accordingly so that trajectories have the potential to achieve the desired conditions. Thus, the HRV of forest structure can assist forest managers who are concerned about restoring habitat structure not only for setting a static goal but also for establishing dynamical views of forest management effects toward their goals.

Fig. 6. Conceptual comparisons between the historical range variabilities (HRV) of live and dead wood biomass under the historical fire regime (gray zone) and the dynamics expected (*a*) in plantations under long-term intensive timber management and (*b*) a hypothetical retention harvest.



This study also illustrates that amounts of dead and live wood do not always follow the same trajectory. The highest amounts of dead wood occur early in succession, following large wildfires and other disturbances. Very low amounts of dead wood probably did naturally occur in stands in the past, but this condition was not common probably because the particular sequences of stand-disturbance events occurred rarely. Information about the HRV of dead wood in different stand-developmental stages could be used to help guide efforts to set goals for dead wood restoration. For example, very large amounts of dead wood would not be typically expected to occur in intermediate stages of stand development, and early stages of stand development typically had very high amounts of dead wood. The characterization of the HRV of dead wood does not imply that HRV should be a goal, but it can provide some context for making management decisions when managers lack a clear ecological rationale.

Conclusions

As forest management shifts towards species and ecosystem goals on some ownerships, managers are faced with the challenge of defining reference conditions and setting clear goals (Grumbine 1994). Given our typically poor understanding of the habitat needs of native species, coarse-filter approaches such as HRV have been suggested as a way to provide a reference distribution that can be used to develop desired future conditions of dynamic forest ecosystems (Landres et al. 1999). In fact, the Forest Service Land Management Planning Handbook (available from www.fs.fed.us/im/directives/fsh/1909.12) identifies the range of variation under historical disturbance regimes as a key component in the assessment of ecological sustainability. Until this study, HRV analyses focused only on broad age-classes of forests, yet many managers are seeking guidance on producing particular structural elements including dead wood (Swanson and Franklin 1992, Brown et al. 2003). Federal managers in the Pacific Northwest often want to know "how much dead wood should I leave or create in this stand?" The answer to this question depends on many factors including the particular wildlife and timber management goals for the stand or watershed and the dead wood conditions of the surrounding landscape. Fire hazard from large accumulations of coarse woody debris, is typically not a concern in this infrequent-fire regime. The wildlife values associated with dead wood are typically of greatest concern. Given that dead wood patterns have been highly altered by past management activities and ownership patterns (Ohmann and Waddell 2002), planners often need a reference point that is based on the potential of a site or landscape, not just its current condition. The method used in this study could be used to evaluate the ecological significance of current patterns and amounts of dead wood in terms of landscape structure and dynamics.

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List of symbols

P_a	Chapman–Richards parameter *a*
P_b	Chapman–Richards parameter *b*
P_c	Chapman–Richards parameter *c*
CMORT	chronic mortality
CONS	dead wood consumption by fire
DECAY	decay rates for deadwood
$\mathrm{FMORT_h}$	high-severity fire mortality
$\mathrm{FMORT_m}$	moderate-severity fire mortality
MFS	mean fire size
NFR	natural fire rotation
SEV	severity of fires

Appendix A

Appendix appears on the following page.

Table A1. The values of the parameters for baseline runs and for the sensitivity runs for (*a*) fire regime and biomass growth and (*b*) decay and chronic mortality rates varied by stand age.

(*a*) Values for fire regime and biomass growth parameters.

			Sensitivity runs	
Parameter	Description	Baseline run	–	+
Fire regime				
NFR_c	Natural fire rotation for coastal zone (years)	200	160	240
NFR_v	Natural fire rotation for valley margin zone (years)	100	80	120
FS_c	Mean fire size for coastal zone (km^2)	73	58.4	87.6
MFS_v	Mean fire size for valley margin zone (km^2)	22.2	17.8	26.6
SDFS_c	SD of fire size for coastal zone (km^2)	320.5	218.1	384.6
SDFS_v	SD of fire size for valley margin zone (km^2)	51	34.9	61.2
SEV(1)	Minimum severity of fires <100 km^2	0	0.0	0.05
SEV(2)	Maximum severity of fires <100 km^2	0.5	0.4	0.55
SEV(3)	Minimum severity of fires 100–500 km^2	0.1	0.01	0.18
SEV(4)	Maximum severity of fires 100–500 km^2	0.8	0.71	0.9
SEV(5)	Minimum severity of fires <500 km^2	0.7	0.535	0.98
SEV(6)	Maximum severity of fires >500 km^2	0.95	0.785	1.0
Biomass				
P_a	Chapman–Richards parameter *a*	700	560	840
P_b	Chapman–Richards parameter *b*	0.02	0.016	0.024
P_c	Chapman–Richards parameter *c*	1.5	1.2	1.8
FMORT_h	High-severity fire mortality*	1	0.9	0.95
FMORT_m	Moderate-severity fire mortality†	0.5	0.45	0.55
CONS_h	High-severity fire wood consumption	0.25	0.2	0.3
CONS_m	Moderate-severity fire wood consumption	0.25	0.2	0.3
DECAY	Decay rates for deadwood	Varies by age (see below)		
CMORT_h	Chronic mortality after highseverity fire	Varies by age		
CMORT_m	Chronic mortality after moderate-severity fire	Varies by age		

(*b*) Values for decay and mortality rates varied by stand age.

			Sensitivity analysis			
	Baseline run		Lower		Higher	
	Coast	Interior	Coast	Interior	Coast	Interior
Decay rates						
Age-class (years)						
0–80	0.05	0.0625	0.04	0.05	0.06	0.075
81–200	0.04	0.05	0.032	0.04	0.048	0.06
201–250	0.035	0.04375	0.028	0.035	0.042	0.0525
251–300	0.03	0.0375	0.024	0.03	0.036	0.045
301–350	0.025	0.03125	0.02	0.025	0.03	0.0375
351–450	0.02	0.025	0.016	0.02	0.024	0.03
451–500	0.022	0.0275	0.0176	0.022	0.0264	0.033
501–550	0.024	0.03	0.0192	0.024	0.0288	0.036
551–600	0.026	0.0325	0.0208	0.026	0.0312	0.039
601–650	0.028	0.035	0.0224	0.028	0.0336	0.042
651–700	0.03	0.0375	0.024	0.03	0.036	0.045
701–750	0.032	0.04	0.0256	0.032	0.0384	0.048
>750	0.035	0.04375	0.028	0.035	0.042	0.0525
Chronic mortality rates (per decade)						
High-severity range						
0–30‡	0	0	0	0	0.1	0.1
>31	0.05	0.05	0.04	0.04	0.06	0.06
Moderate-severity range						
0–20	0.15	0.15	0.12	0.12	0.18	0.18
21–50	0.075	0.075	0.06	0.06	0.09	0.09
>51	0.05	0.05	0.04	0.04	0.06	0.06

Note: Most of the parameter values were varied by ±20% from the baseline values.

*Values varied by –10% and –5% from the baseline values.

†Values varied by ± 10% from the baseline values.

‡Trees are assumed to be too small to be recruited as coarse woody debris. The lower run used the same value as the baseline run.